The Central Nervous System of the Bottlenose Dolphin

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INTRODUCTION

Tursiops is among the most ecologically diverse cetacean genera, with different populations occupying offshore and inshore niches. Inshore groups sometimes spend hours, days, or even weeks in freshwater rivers or lakes connected to the sea while offshore groups may be seen hundreds of miles at sea. The genus *Tursiops* also has a wide distribution: different individuals from various populations might be seen over a north–south range covering about 80% of the distance from the Arctic and Antarctic circles to the equator during the course of a year.

Dolphin brains probably have evolved in response to their ecological niches (Wood and Evans, 1980; Ridgway and Wood, 1988). Since bottlenose dolphins are diverse in distribution, ecology, and adult body size, a comparative study of brain size among adult dolphins of different

bottlenose dolphin populations around the world might shed light on the relationship between brain size, body size, and ecology. I have not completed such a study, but in this chapter I review published information on the brain of the genus *Tursiops* and provide some comparative data with other genera and among a few different bottlenose dolphin populations. In addition, I intend this chapter to guide readers toward the relevant brain literature and introduce them to some of the problems posed by the large, convoluted brain of the bottlenose dolphin (also see Ridgway, 1986a). In this brief discussion, I have not mentioned the thalamus (see Kruger, 1959), the ventricles (McFarland *et al.*, 1969), the fissure pattern of the convexity hemispheres (Morgane *et al.*, 1980), many nuclei such as the red nucleus, the basal ganglia, and other structures. These features are described in some of the literature I have cited.

BRAIN SIZE

In keeping with their diverse body sizes and habitats, cetaceans have variably sized brains, ranging from 200 g in adult franciscanas, *Pontoporia blainvillei*, and susus, *Platanista gangetica*, to a reported high of 9200 g for the largest odontocete, the sperm whale (Kojima, 1951). Although 16 sperm whale brains averaged just over 7800 g and brains of mysticetes can weigh 2600–7800 g, certain species of the family Delphinidae, a group of small- to medium-sized odontocetes which includes the bottlenose dolphin, have the highest brain size to body size ratio among cetaceans. Only in this family have animals with a body size within two or three multiples of human body size attained similar brain weights, for example, *Tursiops* (Fig. 1) about 1500 g, *Steno* 1400 g, and *Lagenorhynchus* 1300 g.

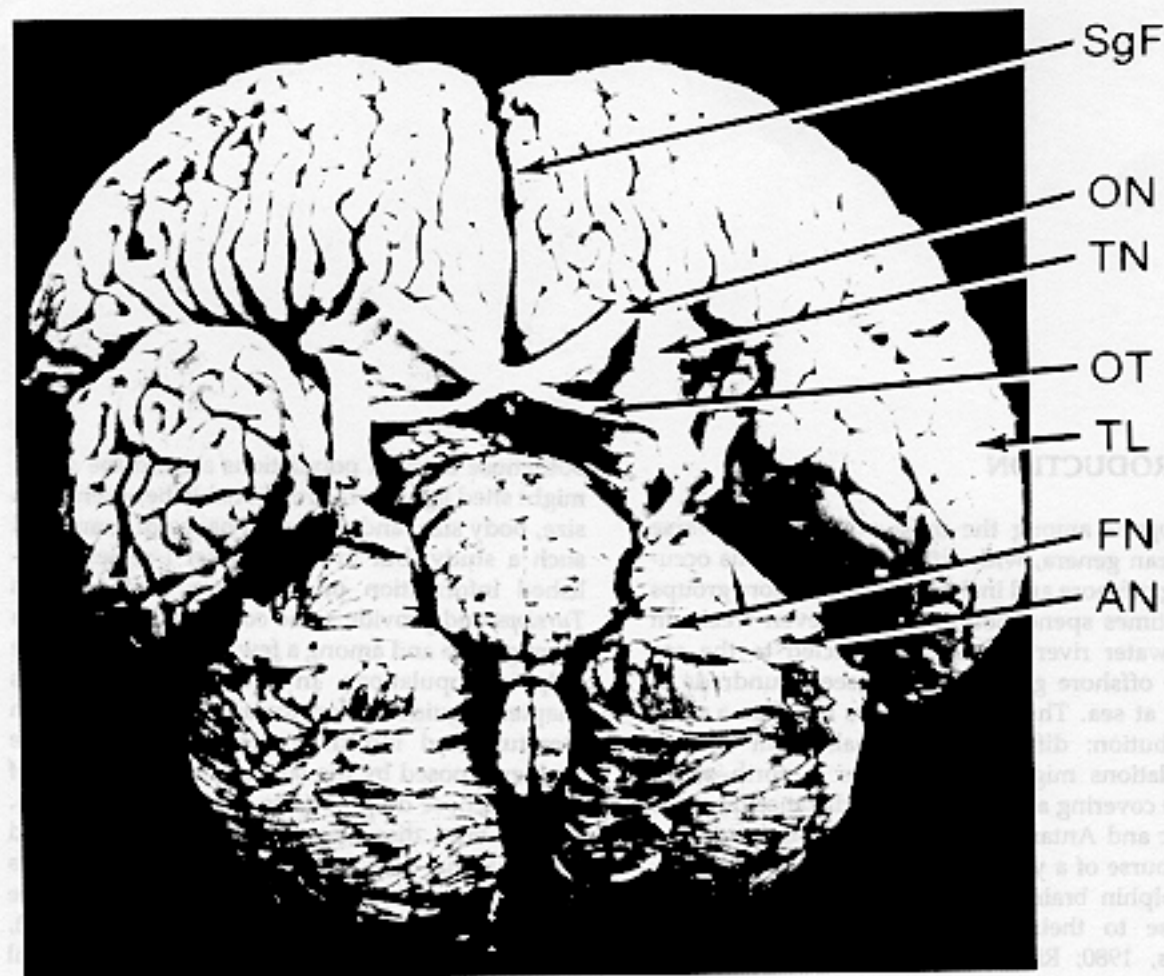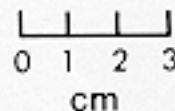The adult male bottlenose dolphin of 172 kg

Figure 1 Ventral surface of the brain of an adult bottlenose dolphin. SgF, Sagittal fissure; ON, optic nerve; TN, trigeminal nerve; OT, optic tract; TL, temporal lobe; FN facial nerve; AN, auditory nerve.

body weight listed in Table 1 had a brain of 1629 g with an encephalization quotient almost four and one-half times larger than an average mammal of the same size (cf. Jerison, 1973; Wood and Evans, 1980). The bottlenose dolphin's closest rival in brain size, other than a few related delphinids and humans, is the gorilla, *Gorilla gorilla*. A male gorilla of 172 kg had a brain of 570 g (Jerison, 1973, p. 393).

While some authors (e.g., Lilly, 1962, 1964) have viewed the large dolphin brain as an indication of high intelligence and possibly even of language capability, others such as Tomilin (1968) have regarded the large dolphin brain simply as an adaptation to a specialized aquatic life. Questions about dolphin intelligence and language remain largely unanswered, and there is no general agreement as to what adaptations to aquatic life could be responsible for a large brain. Sirenians, mammals also totally adapted to an aquatic existence, have relatively small brains.

Some data on brain and body sizes of adult dolphins (Sergeant *et al.*, 1973, list maturity criteria) from the coastal western North Atlantic and Gulf of Mexico, North Pacific, and eastern North Atlantic or Mediterranean Sea are given in Table 1.

BRAINS OF CAPTIVE DOLPHINS

Pilleri (1983) suggested that dolphins' brains shrink as much as 30% when the animals are maintained in captivity. This hypothesis is not based on dolphin data but instead mainly on comparisons of domestic and wild species of land mammals. In reviewing some of Pilleri's sources, I found that the early land mammal studies mentioned in his table had been questioned by Hemmer (1976), who concluded that these studies often were based on unfounded comparisons between wild and domestic groups; for example, domestic animals were compared with species that were not closely related in phylogeny. Moreover, a study by Fram and Stephan (1976) on the tree shrew, *Tupaia glis*, provides evidence which contradicts Pilleri's suggestion that captivity causes a reduction in brain size. Fram and Stephan dissected and weighed the brains of a group of recently trapped wild tree shrews. When they compared these brains to the brains of captive-reared offspring whose parents came from the same population as the wild group, Fram and Stephan found that the brains of the captive-reared tree shrews were significantly larger.

Although Pilleri's hypothesis about captive dolphins appears questionable, it is true that poor nutrition at critical stages of early brain development can result in retardation of brain growth. For example, animals removed from the wild before weaning might be vulnerable to such retardation if their nutritional requirements are not met during the first weeks or months of captivity. In addition, mammalian brain size depends on age. An individual's brain reaches full size just before or soon after sexual maturity and then slowly shrinks. In humans 70–80 years old the brain is more than 100 g smaller, on average, than in 19–20 year olds (Spector, 1956). We know something about the growth of dolphins' brains to maturity (Ridgway, 1986a), but we know nothing of their shrinkage in old age. The question of whether a dolphin's brain shrinks with age can only be answered if careful records are kept on an adequate sample of specimens whose brains are examined and weighed at death.

Because Pilleri's (1983) statement on dolphin brain atrophy has been repeated by others (e.g., Meith, 1985), it prompted me to analyze postmortem records to test whether or not bottlenose dolphins' brains became relatively smaller with increasing numbers of years in captivity. Figure 2 is a regression of body length to brain weight ratio against years in captivity for 18 adult Atlantic bottlenose dolphins. Note that there is no significant difference in this ratio between newly captured animals and those that died after having been in captivity for 5, 10, or more years.

SHAPE AND GROWTH OF THE DOLPHIN BRAIN

In the embryonic stage, the dolphin brain, like those of other mammals, is somewhat oblong in shape (longer than wide) (Kamiya and Pirlot, 1974). By the midfetal stage the odontocete brain appears globular, and by the late fetal stage the brain is wider than long, as it is in the adult (Figs. 1

Table 1
Brain and Body Size of Adult Bottlenose Dolphins[a]

Category	Sex	BdL (cm)	BdW (kg)	BrnW (kg)	Source
E. North Atlantic and Mediterranean		300	240	2.020	Pilleri and Gihr (1970)
		285	200	1.930	Pilleri and Gihr (1970)
		290	220	2.230	Pilleri and Gihr (1970)
		290	220	2.240	Pilleri and Gihr (1970)
		340	250	2.010	Pilleri and Gihr (1970)
	F	296	278	1.886	Weber (1897)
Mean		300	235	2.053	
S.D.		18	25	0.137	
E. North Pacific	M	291	262	1.901	Ridgway (unpublished)
	F	283	255	1.672	Ridgway (unpublished)
	M	261	210	1.555	Ridgway (unpublished)
	M	285	268	1.691	Ridgway and Brownson (1979)
Mean		280	249	1.705	
S.D.		11	23	0.125	
W. North Atlantic coastal	F	240	140	1.588	Kruger (1959)
	F	259	156	1.685	Kruger (1959)
	F	256	154	1.707	Kruger (1959)
	F	240	177	1.558	Ridgway and Brownson (1979)
	F	251	151	1.673	Ridgway and Brownson (1979)
	F	244	164	1.446	Ridgway and Brownson (1979)
	M	257	186	1.849	Ridgway and Brownson (1979)
	M	244	170	1.408	Ridgway and Brownson (1979)
	M	252	152	1.625	Ridgway and Brownson (1979)
	M	240	170	1.524	Ridgway and Brownson (1979)
	F	245	172	1.629	Ridgway and Brownson (1979)
	F	235	120	1.296	Ridgway et al. (1966)
	F	244	160	1.359	Ridgway et al. (1987)
	M	238	165	1.378	Ridgway et al. (1987)
	F	227	140	1.112	Ridgway et al. (1987)
	F	240	145	1.487	Ridgway et al. (1987)
	F	252	197	1.609	Ridgway et al. (1987)
	F	242	225	1.410	Ridgway et al. (1987)
	M	263	198	1.724	Ridgway (unpublished)
Mean		246	165	1.530	
S.D.		8.9	24	0.172	

[a] Data are given for sex, body length (BdL), body weight (BdW), and brain weight (BrnW) of adult bottlenose dolphins from three different geographic areas: eastern North Atlantic and Mediterranean, eastern North Pacific, and western North Atlantic Coastal (including Gulf of Mexico). Specimens from the literature were judged to be mature if they exceeded the mean adult length criteria of Sergeant et al. (1973). Some animals that did not exceed the mean adult length are included because they were determined to be sexually mature by other means. For example, the 227 cm female had two offspring with 10 years intervening between the two. The average bottlenose dolphin female would not be sexually mature at 227 cm.
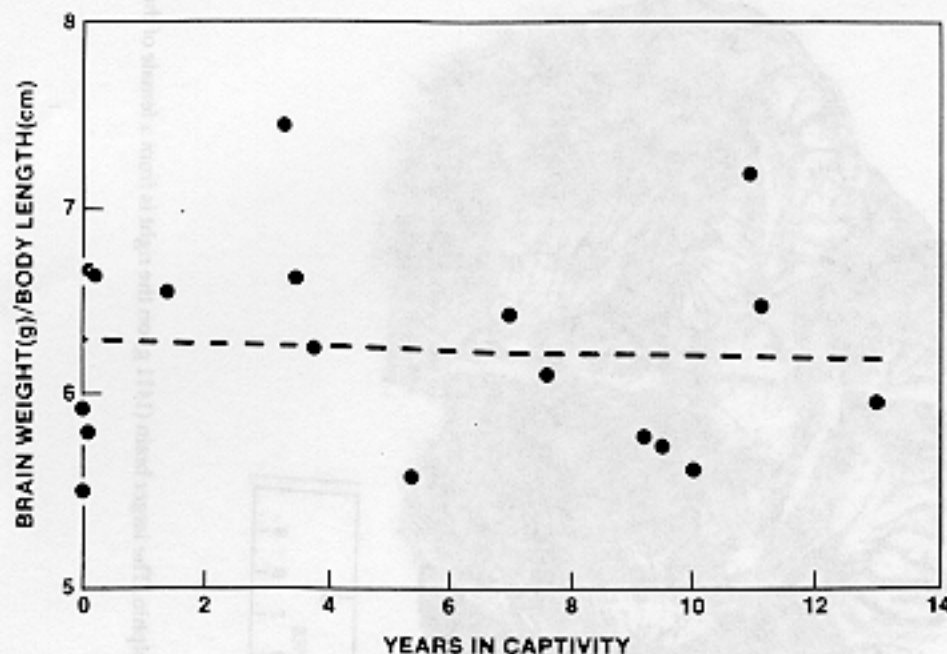
Figure 2   Each point represents the ratio of brain weight to body length for a single bottlenose dolphin brain. The dashed line is a linear regression which shows no significant difference in the brain weight to body length ratio over periods up to 13 years in captivity.

and 3). In postnatal mysticete brains, length and width are more similar. A dolphin brain viewed from the medial aspect of a sagittal section shows that the height is also great compared with the length. An S-shaped curving of the neural axis leaves the axis of the forebrain almost perpendicular to that of the midbrain, giving the impression that the forebrain rotated ventrally during development.

The human brain grows from just under 25% of its adult weight at birth to full development in about 17 or 18 years. J. T. Bonner states, "In man there seems to be an extraordinary prolongation of youth, and this permits the brain to continue its expansion. The period of dependency on parents is increased so that the period when learning can occur becomes relatively long" (Bonner, 1980). Kesarev (1971) has pointed out that human cortex develops mainly in the postnatal years, but that some lower primates are born with cortical forma-

tion about 80% of the adult complement. Kesarev states, "The earliest to appear and the latest to conclude their development in man are those formations of the neocortex which may be considered phylogenetically as the most recent and are associated with the most complex forms of cerebral activity, present only in man, the integrative and analytical functions."

Delphinids are also born with brains at an advanced stage of development. A long gestation period, about 12 months in bottlenose dolphins, is needed so the neonate can swim and engage in activities requiring a more mature brain. In eight Atlantic coastal bottlenose dolphins, neonatal brain weight averaged 42.5% of mean adult weight (Ridgway and Brownson, 1984) (Fig. 3). By weaning age at 18 months, bottlenose dolphin brains are over 80% of mean adult weight, a stage not reached by human brains until 3 or 4 years. Male bottlenose dolphins do not reach sexual maturity
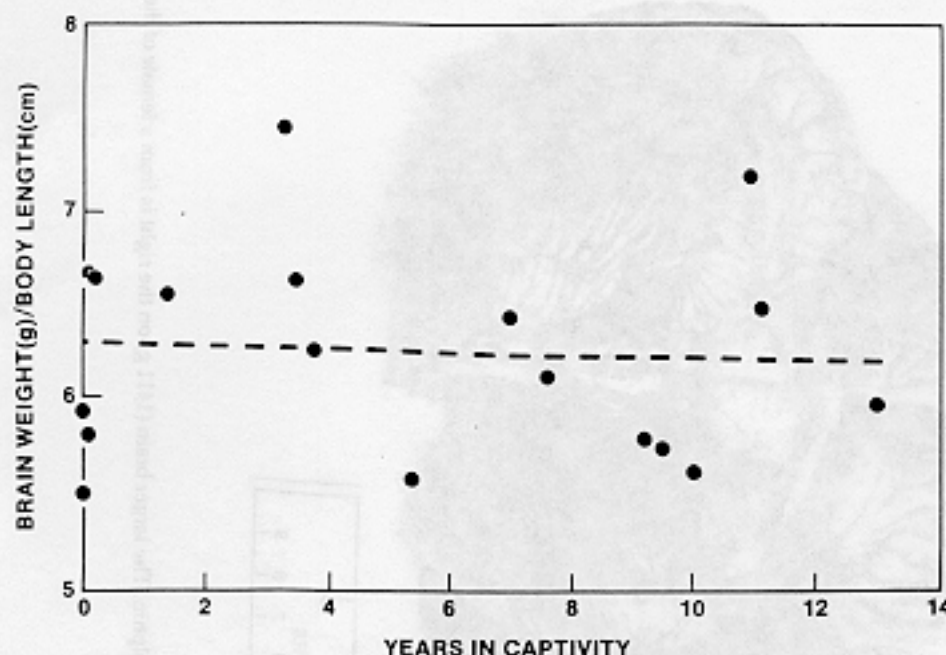
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until about 13 years of age, while females mature somewhat earlier (Sergeant *et al.*, 1973; also see Schroeder, Chapter 25, this volume). From the sparse data available on animals of known age, I estimate that Atlantic coastal bottlenose dolphins reach full brain development in 9 or 10 years, about half the total growth period required for human brains but considerably longer than for brains of most higher mammals.

THE CEREBRAL HEMISPHERES

The greatest expansion in the nervous system in the course of evolution has involved the cerebral hemispheres. The hemispheres of cetaceans are large and enormously convoluted. Although it is often stated that the human brain is the most convoluted of all brains (e.g., Teyler, 1977), odontocetes exceed humans, and all other animals, in convolutedness or fissurization of the cerebral cortex; the cetacean pattern of gyri and sulci is more complicated than in the human cerebral cortex. A much larger proportion of the dolphin's cortical surface is buried beneath the exterior of each cerebral hemisphere. The main sulci that arch along the dorsal and dorsolateral cerebral surface are very deep and incised with microgyri. Toward the core from the sylvian cleft lies an extremely large insula consisting of radial gyri arising fanlike from the transverse insular gyrus, and covered completely by the frontal, parietal, and temporal opercula. In a series of bottlenose dolphins, mean cortical surface area was 3745 cm^2 compared with 2275 cm^2 in a similar number of human brains (Elias and Schwartz, 1969; also see Haug, 1969, 1970; Ridgway and Brownson, 1984); however, the dolphin's cortex was 1.3–1.8 mm in thickness, considerably thinner than the human cortex which is about 3.0 mm thick. The total volume of bottlenose dolphin cortex was about 80% of that found in humans.

In cetaceans, the most primitive of neocortical regions (Kesarev, 1969), the limbic lobe, is extensive, although the hippocampal formation is much smaller than that of man. In the bottlenose dolphin's limbic lobe, the total number of cells is greater than in the limbic lobe formations of primates, including man (Morgane *et al.*, 1982).

Nevertheless, the limbic lobe of the dolphin brain is relatively small compared with the remainder of the neocortex. In the common dolphin, *Delphinus delphis*, Filimonoff (1965) found that periarchicortex constituted about 0.4% of total neocortical surface area as compared with 1.3% in man, 2.7% in dog, and 17.6% in hedgehog, *Erinaceus*. Although these percentages are quite different in dolphin and hedgehog, some authors have drawn parallels in brain structure between these very remotely related mammals based on microstructure and lamination characteristics of the cerebral cortex (Kesarev and Malofeyeva, 1969; Morgane *et al.*, 1986; Glezer *et al.*, 1988).

Following principles of brain organization established by Filimonoff (1949, 1965), Kesarev and Malofeyeva (1969) have suggested that the ancestors of dolphins left land for the sea 70–90 million years ago, before land mammals developed many modern features of brain structure. These authors have pointed out various similarities in brain microstructure and organization between dolphins and primitive insectivores such as the hedgehog. Morgane and associates (1986), who have done even more extensive histological studies, agreed with Kesarev (1969) and suggested that the cetacean cortex as a whole does not appear to have reached the latest stage of cortical evolution, retaining all the conservative characters seen in primitive terrestrial and aerial forms such as hedgehogs and bats. Cortical layer IV (granular layer) is absent or at least difficult to identify. Areas of cortical surface identified as primary sensory cortex by physiological mapping studies are agranular and not distinguished on histological grounds as primary sensory cortex. Glezer *et al.* (1988) elaborated these ideas into an initial brain hypothesis, which holds that the dolphin brain is the result of repeated elaboration of a primitive "initial brain," contrasted with more complex development seen in the brains of land mammals, especially primates.

Proponents of the initial brain hypothesis have generally placed the move of ancestral cetaceans from land to sea much earlier than the fossil record indicates (see van Valen, 1966; Gingerich *et al.*, 1983), and very little independent evidence supports the proposed cetacean–insectivore connection (Ridgway and Wood, 1988). We suggested that brains of cetaceans have evolved in response

to their various ecological niches and that the ancestors of cetaceans entered the sea to take advantage of its rich food resources after they had developed large bodies and a predatory lifestyle on land, in marked contrast to the small insectivores. Ridgway and Wood (1988) proposed that to the extent that ontogeny recapitulates phylogeny (Gould, 1977), developmental studies on the cetacean brain would seem to be a rewarding approach toward understanding dolphin brain phylogeny. Garey and Leuba (1986) reported finding a thin layer IV in the visual cortex of two young bottlenose dolphins, one 3 years of age and the other 18 days old. Layer IV was absent in brains of animals age 12, 22, 26, and 33 years. If these findings hold up, they suggest that granular layer IV is a regressing characteristic of cetacean brain evolution and would not seem compatible with the initial brain hypothesis.

As mammalian brains increase in size, the neuron density decreases. According to at least three studies (Hawkins and Olszewski, 1957; Tower, 1954; Morgane et al., 1982), the ratio of glial cells per nerve cell is correlated directly with brain size. In mice, the glial/neuron ratio is around 0.2, in humans approximately 1.8, in bottlenose dolphins about 2.1, and in fin whales, Balaenoptera physalus, 4.5. Thus, there is at least a 20-fold decrease in neuron density from mouse to whale.

THE CORPUS CALLOSUM

The corpus callosum (CC) is a large bundle of nerve fibers that connects the two cerebral hemispheres. These fibers apparently are important communication links between the two hemispheres and are necessary for transmission of learned behavior from one hemisphere to the other (Myers, 1956).

Although the average adult bottlenose dolphin has a brain weighing more than that of the average adult human, the CC of the dolphin brain is considerably smaller. Nieto et al. (1976) measured the cross-sectional surface area of the CC in a smaller brained dolphin Stenella graffmani (Stenella attenuata, the pantropical spotted dolphin, Perrin et al., 1987). The dolphin brain of 832 g was compared with a human brain of 1085 g. The cross-sectional surface area of the human CC was 991 mm^2 compared to 180 mm^2 for the S. graffmani CC. The CC of the larger bottlenose dolphin brain probably has more cross-sectional area; however, even if brains of identical size were compared, I estimate that the bottlenose dolphin CC has no more than about one-quarter the cross-sectional area of the human CC.

The finding of a smaller cross-sectional area of the dolphin CC leads me to conclude that the dolphin CC is made up of fewer total fibers or that the average fiber diameter is much smaller. This in turn implies that, in comparison with the human brain, communication between hemispheres is at a reduced overall level owing to fewer fibers or is slower because of smaller fiber diameters. Either condition would result in greater hemispheric independence and probably a lesser degree of hemispheric coordination in the dolphin brain.

DOLPHIN BRAIN METABOLISM

Hockett (1978) states, "Brains are metabolically expensive and don't get bigger (phylogenetically) unless in some fashion they are more than paying for their upkeep." This statement, supported by measures of brain metabolism in many vertebrates, gives rise to these questions: Might the cetacean brain represent a departure from this general trend? Could the dolphin brain be large, but metabolically less active than the brains of other mammals?

Many authors have found that dolphins have a higher metabolic rate than average terrestrial mammals of similar size (Irving et al., 1941; Pierce, 1970; Ridgway and Patton, 1971; Hampton et al., 1971). Opposing evidence has been presented by Karandeeva et al. (1973) and Lavigne et al. (1986), who contend that bottlenose dolphins do not have high rates of metabolism. I am skeptical of the results published by Karandeeva and colleagues because I question their method: they employed a mask and rubber bag placed over the blowhole to collect expired air from Black Sea bottlenose dolphins, later measuring the volume and oxygen content with a gasometer. Karandeeva et al. (1973) reported mean respiratory volumes ranging from about 18 to 23 ml/kg, values less than half those

reported by Irving *et al.* (1941) and Ridgway *et al.* (1969) for Atlantic bottlenose dolphins and by Kooyman and Cornell (1981) for Pacific bottlenose dolphins. Their measures of oxygen consumptions are therefore equivalently reduced. Based on my own experience in trying to collect bottlenose dolphin lung volume with a mask and rubber bag, I suspect the difference in reported oxygen consumption values between Black Sea and Atlantic bottlenose dolphins may be methodological. Lavigne *et al.* (1986) gave more credence to the Karandeeva data for bottlenose dolphin metabolic rates than to the measurements reported by others (cited at the beginning of this paragraph). In addition, I doubt the findings of Lavigne *et al.* because they employed allometric methods, procedures which I believe may be questionable [see reviews by McNab (1988) and Smith (1984)], with respect to scaling the rate of metabolism and applying such scaling to individual species.

In addition to oxygen consumption data, there is other evidence for a high rate of metabolism. The high-protein diet (dolphins consume almost no carbohydrates) contributes considerably to a high metabolic rate. Bottlenose dolphins have large thyroid glands (Harrison, 1969) and a high level of circulating thyroid hormones (Ridgway and Patton, 1971). Long-term food consumption of captive animals correlates well with observed levels of oxygen consumption. The bottlenose dolphin studied by Ridgway and Patton (1971) required over 6000 k cal/day to maintain body weight. Even higher levels of daily caloric consumption have been reported by other authors (Shapunov, 1973; Van Dyke and Ridgway, 1977; Cates and Schroeder, 1986).

Bottlenose dolphins are diving mammals with the demonstrated capability to reach depths as great as 547 m (see Ridgway, 1986b, for a review of diving depth studies) and to remain submerged for more than 7 minutes. Alveolar gas tensions after long dives by Atlantic coastal bottlenose dolphins (Ridgway *et al.*, 1969) suggest that the brain may be capable of short periods of anaerobic metabolism, a capability not found in adult land mammals that have been studied. Since this observation in bottlenose dolphins, anaerobic metabolism by the seal brain has been demonstrated during the later stages of a maximal dive (Kerem *et al.*, 1971; Simon *et al.*, 1974).

I was unable to confirm anaerobic metabolism during hypoxic periods of up to 6 minutes in anesthetized dolphins. Arteriovenous differences in oxygen and glucose across the dolphin brain were as great as or greater than those in the brains of anesthetized humans. Based on my own data and those of Soviet researchers, I conclude that there is no basis for assuming dolphin brains have a lower overall rate of metabolism than do human brains. The great fissurization of the dolphin brain creates a large cortical surface area; the large area may be essential to provide sufficient surface contact with the abundant meningeal blood supply (Wilson, 1933; Ries and Langworthy, 1937), supporting the cortex's need for oxygen. The view that brain size and fissurization in odontocetes are related to diving and the need to sustain brain function during prolonged hypoxia is, however, weakened by the observation that seals (Scholander, 1940) and sirenians (Scholander and Irving, 1941), two groups of animals that also dive for long periods, have smaller, less convoluted brains and a thicker cortex.

THE VISUAL SYSTEM

Bottlenose dolphins have well-developed optic nerves and large eyes, and they appear to have good vision. Rods and cones are present in the retina. However, there is no distinct fovea centralis, the retina is thick, and a layer of giant ganglion cells (cell bodies up to 150 μm in diameter) appears to serve most of the central retina. These giant ganglion cells support giant dendrites and myelinated optic nerve fibers that range up to 8 or 9 μm in diameter (Dawson *et al.*, 1982).

In most mammals, each eye projects the majority of its nerve fibers to the opposite (contralateral) cerebral hemisphere; however, considerable numbers of fibers project to the cerebral hemisphere on the same side (ipsilateral side). The dolphin may be an exception to the general rule that crossed and uncrossed fibers arise from each eye. Each of the dolphin's eyes probably projects only to the contralateral hemisphere. This conclusion is somewhat tenuous because it results mainly from two anatomical studies of one animal each. First, Hatschek (1903, 1960) studied the brain of a captured

dolphin that had lost one eye. Using a Weigert-stained series of brain stem sections, he observed total decussation of the optic nerve across the optic chiasm. From this information, he concluded that dolphins lacked binocular vision. Second, Jacobs et al. (1975) described a silver degeneration study carried out on a male bottlenose dolphin that had been enucleated and then vitally perfused after surviving for 14 days. With some reservations concerning the long survival time and the 19% discrepancy between numbers of fibers in the optic nerve and optic tract of their specimen, the researchers concluded that the dolphin exhibited an apparently total decussation of optic nerve fibers, a condition atypical of mammals but common in other vertebrates.

Some physiological evidence also supports complete crossing of optic nerve fibers. Supin et al. (1978) mapped the sensory projection zones on the dorsal and dorsolateral surface of dolphin cortex. They found that large evoked potential responses were obtained from visual cortex when light flashes were presented to the contralateral eye, but no such responses were obtained when equivalent flashes were presented to the ipsilateral eye.

Although certainly incomplete, the anatomical and physiological evidence suggests that dolphins do not have binocular vision. Langworthy (1932), like Hatschek (1903, cited in Breathnach, 1960), doubted that bottlenose dolphins had stereoscopic vision, stating that "the development of the visual cortex compares well with that described by Mott for other mammals having panoramic vision." It appears to me that bottlenose dolphins have some degree of visual overlap ventrally and rostrad as well as dorsally and slightly caudad. Despite these small areas of overlap in the visual field, the eyes appear to move independently. McCormick (1969) observed that one eye might look forward and dorsally, while the other might look rearward and ventrally. Dawson et al. (1981) reported a physiologic investigation which confirmed that dolphin eye movements are not conjugate. Power spectral density analyses of dolphin eye movements showed maximal power around 0.1 Hz, lower than the human counterpart (Dawson et al., 1981).

The dolphin corneal reflex appears well developed, and the pupil reacts to light. The retractor bulbi is large, and the other extrinsic ocular muscles are present and well developed. The oculomotor nerves are small compared with the fifth, seventh, and eighth cranial nerves but are by no means rudimentary. The presence of an Edinger-Westphal nucleus is questionable. Description of the oculomotor nuclei has been complicated by the presence of a large encapsulated group of cells just dorsal to the third nucleus, the nucleus ellipticus (Breathnach, 1960).

In other mammals, except elephants and possibly seals, the mesencephalic elliptic nucleus apparently has no homolog. The nucleus appears to represent an extensive bilateral elaboration of ventral and ventrolateral periaqueductal gray matter. In at least two studies (see Breathnach, 1960) of odontocetes, the nucleus was described as consisting of a larger dorsal part and a smaller ventromedial portion. One report suggested that the medial portion of the elliptic nucleus contributed fibers to the third nucleus and that the dorsal part possibly corresponded with the nucleus of Darkschewitsch of other mammals. Fibers from the elliptic nucleus have been traced in a caudal direction in a large medial tegmental tract as far as the rostral levels of the inferior olivary complex.

The functional significance and anatomical connections of the nucleus ellipticus, an unusual structure of the cetacean brain, remain obscure. A parallel has been drawn between the complex nasal sac structure of dolphins and the large trunk of the elephant, suggesting that in each the nucleus ellipticus may be involved in innervating nasal musculature (Breathnach, 1960). However, the nucleus ellipticus appears to have no clear connections to the facial complex; its association with the mesencephalic reticular formation, a matrix of tracts and specific nuclei, perhaps makes identification of definite connections more difficult.

The superior colliculus forms an obvious prominence in all cetacean species. In many, such as bottlenose dolphins, the superior colliculus is much smaller than the inferior (acoustic) colliculus, a reversal of the size relationship seen in humans and other land mammals. The lateral geniculate is readily identifiable, but in bottlenose dolphins and common dolphins at least, there is reported to be no true lamination such as there is in mammals with binocular connections (Kruger, 1959, 1966). Mapping studies by Soviet investigators have located visual cortex not at the occipital

pole, but in a superior and medial position high in parietal cortex (Supin *et al.*, 1978).

DOLPHIN SLEEP

Shurley *et al.* (1969; see also Serafetinides *et al.*, 1972) were the first to find evidence supporting Lilly's (1964) claim that cetaceans could sleep with half the brain awake. More extensive research by Soviet investigators found marked asymmetries in electroencephalograms (EEG) from right and left hemispheres of bottlenose dolphins (Mukhametov *et al.*, 1977, 1987; Mukhametov, 1984). Mukhametov (1984) recognized three stages in the dolphin EEG: stage 1, desynchronization; stage 2, intermediate synchronization including sleep spindles and theta and delta waves; and stage 3, maximal synchronization, when delta waves of maximal amplitude occupied not less than 50% of each scoring interval. Stages 1 and 2 occurred bilaterally or unilaterally. Stage 3 occurred in only one hemisphere at a time. Wakefulness or bilateral EEG desynchronization (EEG stage 1 in both hemispheres) occupied 50–60% of the recording time. Stage 2, intermediate synchronization, was sometimes recorded bilaterally, and at such times dolphins displayed EEG patterns typical of terrestrial mammals. Mukhametov *et al.* (1987) report, "The whole sequence of respiratory movements of dolphins may be observed during bilateral intermediate EEG synchronization without arousal." Bilateral intermediate EEG synchronization (stage 2 in both hemispheres) occupied only a small percentage of the recording time. Unihemispheric slow-wave sleep (stage 3 in only one hemisphere), the main type of sleep observed in the dolphin brain, occupied 30–40% of recording time. It was stated (Mukhametov, 1984),

> We have never recorded bilateral delta waves in the dolphin brain during natural sleep. The unilateral sleep episodes can last more than 2 h. . . . Simultaneous recordings from the parietal, occipital, and frontal fields of the hemispheres confirm that a hemisphere is always synchronized or desynchronized as a unit. Records from thalamic nuclei demonstrate that the thalamus can also generate slow wave activity unilaterally and concurrently with the ipsilateral neocortex. Thus, uni-

lateral slow wave sleep is not only a cortical, but also a subcortical phenomenon.

In the most recent paper on bottlenose dolphins by the group (Mukhametov *et al.*, 1987), they quantified sleep studies of several days' duration. Based on EEG signs, the dolphins spent an average of 33.4% of each day asleep.

Dreams certainly can be regarded as mental events, and dreaming in humans has been firmly connected to physiological events described as rapid eye movement sleep (REM). REM (also called paradoxical or dream sleep) has been reported in many mammals, but in the dolphin there is definitely room for controversy about its presence. Mukhametov (1984) states flatly that he has never observed REM in many days and nights of recording dolphin EEG, involving 30 experimental subjects over a period of 8 years: "*Tursiops truncatus* and *Phocoena phocoena* are with the echidna among the three species in which no paradoxical sleep has been revealed. It is noteworthy that the echidna is a secondary terrestrial mammal and its ancestors were aquatic mammals" (Mukhametov, 1984; the basis for the assertion that the echidna is a secondary terrestrial mammal is not given). Six minutes of REM was observed in a single night's recording of a pilot whale, *Globicephala macrorhynchus* (Shurley *et al.*, 1969). Flanigan (1974, 1975) observed bottlenose dolphin male nocturnal erections during apparent sleep, a sign of REM in man and other mammals.

BLOOD SUPPLY TO THE BRAIN

In most mammals the internal carotid artery is the major supplier of blood to the brain. This is not the case in dolphins. Their brains are supplied through the massive thoracicospinal retia (Viamonte *et al.*, 1968). In its course from heart to brain, blood passes through the retia. This arrangement is thought to have a pressure-damping function for the cerebral circulation (Nagel *et al.*, 1968). Neither the internal carotid artery nor vertebral arteries supply blood to the dolphin brain, and the circle of Willis is absent (McFarland *et al.*, 1979). The entire cerebral blood supply comes through a thoracicospinal rete, supplied by intercostal and posterior thoracic arteries.

bottlenose dolphins in three different tanks at Point Mugu, I found that switching the direction of water current in the pool, after the dolphins' swimming direction had been well established, did not change the direction of swimming.

Soon after capture the bottlenose dolphins swam almost continuously, even while apparently asleep; however, as time passed most of the dolphins ceased this continuous swimming and settled into a surface hanging behavior (see McCormick, 1969; Ridgway, 1972; Flanigan, 1974) during periods of rest or sleep. I have observed six females, adapted to such surface hanging behavior, that became pregnant and delivered live offspring; in each case, the surface hanging behavior ceased immediately after parturition, and mother and calf swam continuously in a counterclockwise circle. Only occasionally did the animals reverse direction. Females that had relatively straight dorsal fins developed a distinct leftward tilt in the fin as did their offspring. The majority of bottlenose dolphins at Sea World in San Diego had left-tilted dorsal fins and swam counterclockwise (L. H. Cornell, pers. commun., 1984).

According to Balonov et al. (1981; also see Harnad and Doty, 1977) the direction of rotational tendencies indicates greater activity of the opposite hemisphere. When dolphins swim in a counterclockwise direction, the rotational tendency is toward the left and away from the right hemisphere, presumably the one with greater activity. Those dolphins that circle while asleep should have alternation of activity between the hemispheres according to the findings of Soviet investigators (Mukhametov et al., 1977; Mukhametov, 1984); yet they do not change the direction of circling. These findings seem to confound the idea that the dolphins turn in the opposite direction from the hemisphere with greater activity.

Eye Preference

In 1964, Adolph Frohn (then of the Miami Seaquarium and an early dolphin trainer who trained at the first oceanarium, Marine Studios of Florida) told me, referring to bottlenose dolphins, "A porpoise has a looking eye and it is more often the right one." I have not made a thorough study of eye preference, but in observing 27 recently captured bottlenose dolphins, I noted that 19 approached and examined my outstretched hand with the right side and eye facing me. Right eye preference is by no means universal, and the animals often appear to attend the trainer with both eyes. In the early stages of training, the dolphin often stations in front of the trainer; since the majority of trainers are right-handed, the dolphin might be expected to develop a bias toward the left eye.

Right eye preference seems consistent with the counterclockwise swimming that we observe in the majority of captive dolphins. This direction of swimming places the right eye toward the enclosure wall and toward any human outside the tank who might provide food, other reward, or stimulus. Since the optic chiasma is completely crossed, right eye preference may suggest a leading role for the left hemisphere in vision, whereas the counterclockwise turning might suggest a leading role for the right hemisphere in that movement. The case for counterclockwise turning is certainly much stronger than that for right eye preference.

With captive bottlenose dolphins that I have observed, the neonate, especially in the hours soon after birth, usually swam on the mother's left, the side away from the enclosure walls, as she swam counterclockwise. This may be a manifestation of the mother's desire to keep the neonate away from the tank wall and other outside influences such as people. In the wild, priorities might be different. Maxwell (1960) observed wild bottlenose dolphins with calves off the coast of northern Scotland, noting that the calves swam to the right of the mothers.

THE TERMINAL NERVE, OLFACTORY APPARATUS, AND CRANIAL ASYMMETRY

Kellogg (1928) suggested that during the aquatic evolution of the odontocetes, the olfactory nerves were effectively shut off from the narial passages and did not survive the rearrangement of the skull and migration of the nasal opening to the top of the head. Neurologists have questioned Kellogg's idea (e.g., Edinger, 1955). At this time, we are still lacking an entirely satisfactory explanation for the

absence of the peripheral olfactory apparatus. In early fetal stages, the olfactory bulb, nerve, and tracts are present. As the fetus develops, the structures degenerate, and they are completely absent from mature odontocete brains. Although the more peripheral olfactory components of the cetacean nervous system are absent or rudimentary, other brain structures traditionally thought to be involved in olfaction are present in the mature dolphin. The olfactory lobes and septal areas are large; the hippocampus and subiculum are small. The well-developed entorhinal cortex is more anteriorly located in the temporal lobe, and the presubiculum is more posterior than in other mammals; in general, the rhinencephalon displays the same basic structural arrangement as in primates or carnivores (Breathnach, 1960; Jacobs et al., 1971). The seemingly paradoxical presence of a "nosebrain" without peripheral connections or sensory olfactory endings is one of the more intriguing features of the cetacean central nervous system. Despite the complete absence of olfactory nerves in adult odontocetes, the tiny terminal nerves that have been observed to accompany the olfactory nerves in many vertebrate species are present in fetal and adult dolphins (Figs. 4 and 5).

Toothed whales, but not baleen whales, generally have an asymmetrical cranium (Ness, 1967; Rommel, Chapter 2, this volume). The nasal opening is shifted to the left of the cranial midline to varying degrees, and several skull and head structures on the right are larger than those on the left. There is no known reversal of the family-specific asymmetries on the part of any individual odontocete. A few early authors reported asymmetries of the brain (see review by Breathnach, 1960). These observations often have been discounted because of the possibility that such large brains might be liable to deformation during long periods of fixation. However, Ridgway and Brownson (1984), using freshly fixed material, found significant differences in the surface area of cerebral cortex between left and right hemispheres in bottlenose dolphins. The right hemisphere had a significantly greater surface area.

The asymmetry of the odontocete skull is apparently the result of the enlargement of dorsal elements on the right side. In bottlenose dolphins (and most other odontocetes), the blowhole is shifted to the left of the midline; the nasal plug,

nasal-plug muscle, premaxillary sac, premaxillary fossa, and nasofrontal sacs are all much larger on the right. Wood (1964) proposed that the cranial asymmetry related to the development of a sound-producing organ and represented a modification of the skull having to do with echolocation (see also Wood and Evans, 1980).

Sleptsov (1939) proposed another interesting explanation for the asymmetry of the skull and brain of odontocetes based on his studies of common dolphin, white whale, Delphinapterus leucas, and harbor porpoise, Phocoena phocoena, embryos. Sleptsov found, in the dolphin embryo, that the left olfactory nerve and lobe degenerate more rapidly than those on the right, resulting in the cerebral and cranial asymmetries.

Johnson (1914) reported that the terminal nerves or nervus terminalis (nT) were present in the harbor porpoise. From a single gross specimen he illustrated seven strands running in the pia on the ventromedial surface of the frontal cortex of one cerebral hemisphere. This brain had been removed from the cranium by someone else, and Johnson could only describe the strands to the point on the frontal brain surface where they had been cut off (see Fig. 4). Sinclair (1951a,b) first described the dural part of nT, the large stellate ganglia (see Fig. 5). Having only a skull of a bottlenose dolphin from which the brain had been removed, Sinclair described the ganglia as being large and asymmetrical, and he illustrated the left ganglion as being 3 mm wide. [Sinclair called the species he studied a "porpoise." At least one recent report (Oelschläger and Buhl, 1985) has mistakenly inferred that Sinclair's specimen was from a harbor porpoise. In Europe, the term porpoise is used almost exclusively for the harbor porpoise and its close relatives; however, this usage of cetacean vernacular names does not hold in the United States. Harbor porpoises are absent from the Texas coast where Sinclair obtained his specimen, but bottlenose dolphins are common there and are usually called porpoise locally. Furthermore, Sinclair's notes in the Blocker History of Medicine Collections, Moody Library, University of Texas Medical Branch, Galveston, indicate that his porpoise specimens were bottlenose dolphins.] Sinclair was apparently unaware of Johnson's work on the harbor porpoise, since he did not cite the earlier observation. Yoshikawa and Nakamura
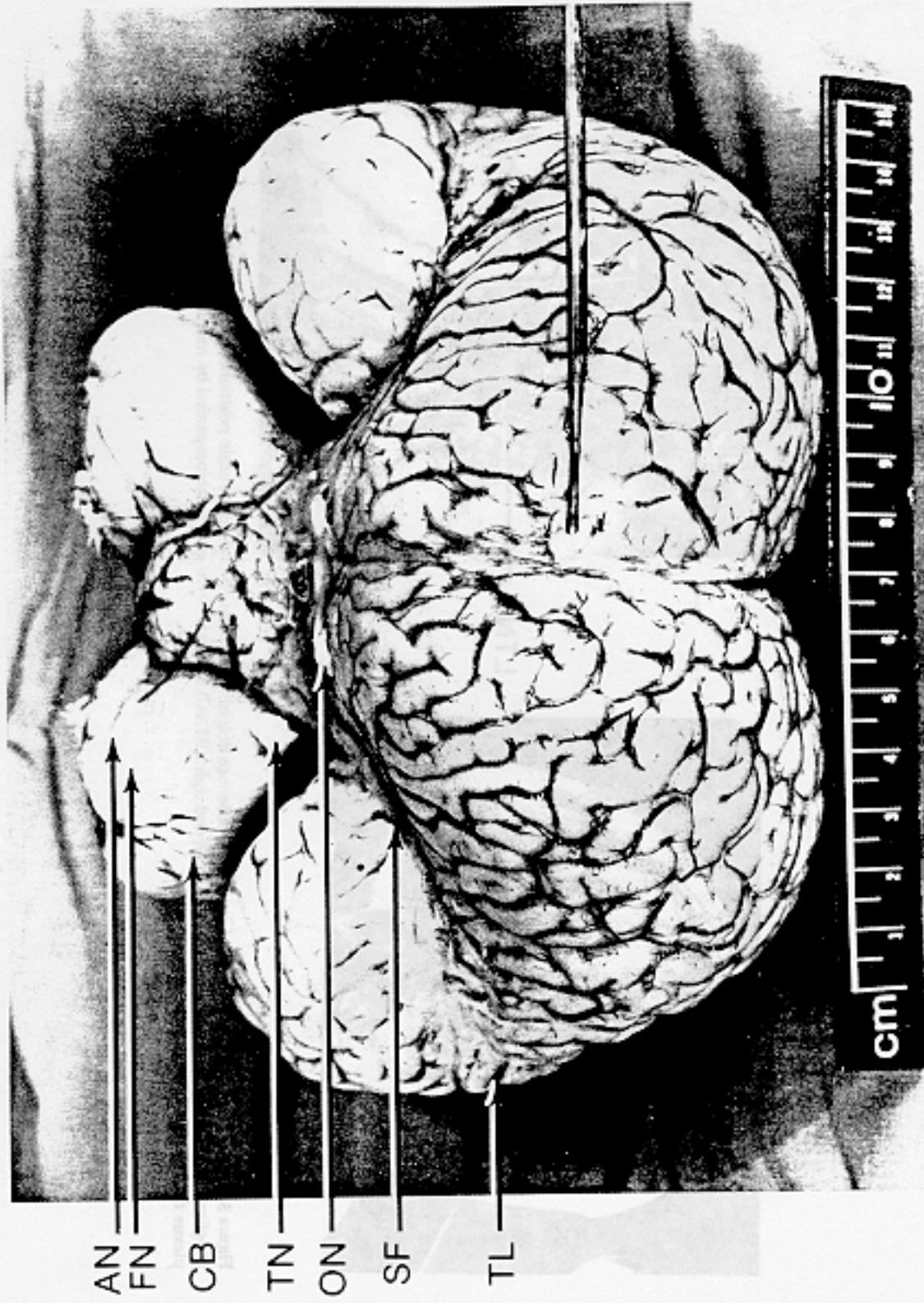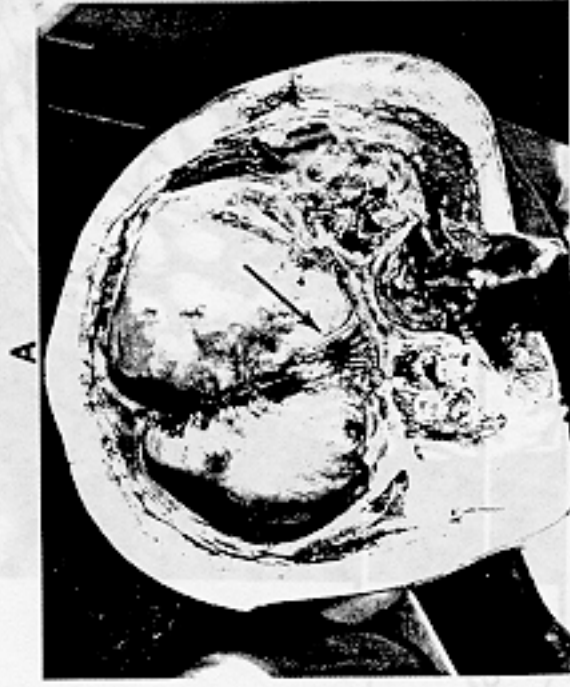
Figure 4 Anterior aspect of a bottlenose dolphin brain (ventral surface up). The probe points to a strand of the right terminal nerve. TL, Temporal lobe; SF, sylvan fissure; ON, optic nerve; TN, trigeminal nerve; CB, cerebellum; FN, facial nerve; AN, auditory nerve.
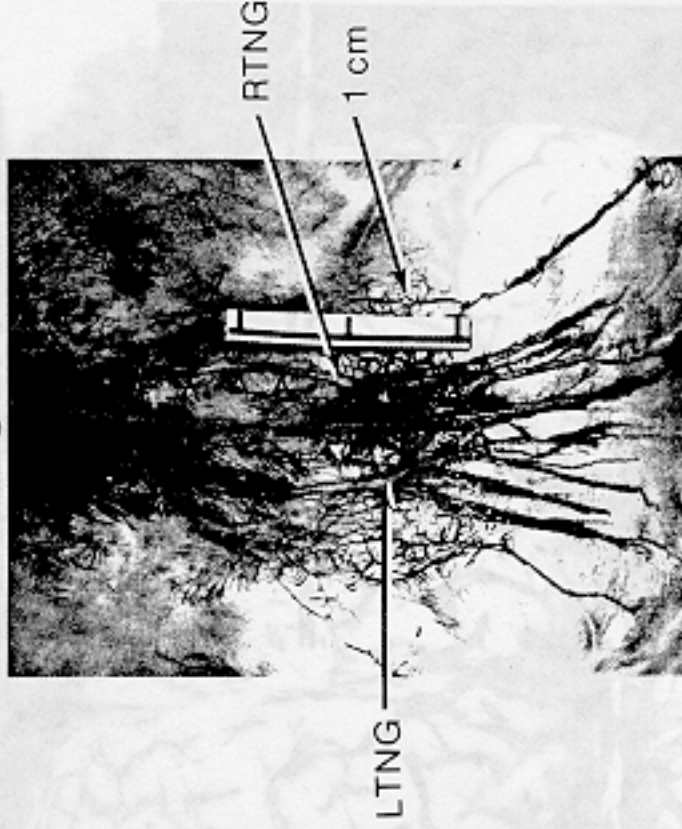
Figure 5 (A) Section through the cranial vault of a bottlenose dolphin. The arrow points to the scale positioned just lateral to the right terminal nerve ganglion. (B) Closeup of A showing the left (LTNG) and right (RTNG) terminal nerve ganglia accompanied by numerous blood vessels of the vascular plexus that courses through the area.

(1952) found in the bottlenose dolphin what Johnson (1914) had found in the harbor porpoise; they traced nT strands about 7.5 cm, concluding that the nervus terminalis very likely goes into the brain just anterior to the optic fasciculus.

Sinclair (1966) studied the development and subsequent atrophy of the olfactory complex in the delphinid genus *Stenella*. In a 27-mm embryo, he traced the nT into the olfactory bulb. He found that later in development the olfactory bulb atrophies, leaving the nT alone coursing through the cribriform area. Buhl and Oelschläger (1986) identified the nT system in embryos of several species of odontocetes. In this study and in an earlier series on the olfactory system of the embryonic harbor porpoise (Oelschläger and Buhl, 1985), they found no evidence of a vomeronasal system. Thus, it appears that of the trio of nerve complexes that course through the cribriform area in most mammals—olfactory, vomeronasal and terminal—only the terminal nerve system survives in odontocetes.

The nT ganglia of the bottlenose dolphin are large (Fig. 5) and contain several thousand cells each. There are at least two large myelinated neuron types, round cells 30–50 μm in diameter and elongate fusiform cells about 15 μm across (Ridgway et al., 1987). Many of the fusiform cells contain luteinizing hormone-releasing hormone (LHRH), which has been observed in terminal nerves of various species and has led some observers to suggest that the nT influences sexual reproduction (Demski and Schwanzel-Fukuda, 1987). The nT ganglia of toothed whales are the largest nT structures so far identified and to me suggest an intriguing evolutionary question: Why did the terminal nerve survive the migration of the nares to the top of the head when the olfactory nerves did not?

THE GUSTATORY SENSE

Because dolphins are regarded as anosmic, because the animals usually swallow fish and other food whole without mastication, and because, until recently, taste buds had not been found in the tongue of several dolphin species, some ce-

tologists have doubted that the animals possess the sense of taste. A presumed gustatory nucleus of the thalamus and the elaboration of the seventh and ninth cranial nerves suggested to neuroanatomists, however, that the gustatory sense is well developed (cf. Kruger, 1959).

Histological studies have produced descriptions of taste buds within five to eight pits that form a V-shaped row on the posterior dorsum of the tongue (Donaldson, 1977; Yamasaki et al., 1978). In one study of *Stenella coeruleoalba*, taste buds were found in the tongue pits of young dolphins but not in those of adults (Yamasaki et al., 1978); in another study, a nerve supply to the buds could not be demonstrated (Donaldson, 1977). There still seems room for doubt that cetaceans have taste buds such as those present in man and most other mammals. Nonetheless, there appears to be psychophysical evidence for chemoreception by sensors in the tongue or mucous membranes of the mouth since trained bottlenose dolphins reportedly can detect chemicals dissolved in seawater (Nachtigall and Hall, 1984). More study is needed on the epithelium and sensory endings of the tongue and oropharynx and especially on the V-shaped row of pits found in the tongue of dolphins.

In most mammals, the facial nerve, which is well developed in cetaceans, attends taste to the anterior two-thirds of the tongue and carries secretomotor fibers to salivary glands. Pores of glands present within the pits, and numerous gland orifices clearly visible on the dolphin tongue and oropharynx, secrete a viscous mucoid material which does not readily dissolve in water. The presence of salivary glands has been doubted by several authors (see Breathnach, 1960), although it is possible that some of the small glands in the tongue or pharyngeal area are salivary. For animals with a diet almost completely devoid of carbohydrates, and which swallow their food whole, the absence of salivary secretion would not seem a great handicap. In dozens of dissections, I have not found salivary glands in the bottlenose dolphin; moreover, I have observed that a triangular structure along the dorsal margin of the mastohumeralis muscle, identified as a parotid salivary gland in at least one earlier report on the pilot whale (Murie, 1874), has the histological structure of a lymph node.

THE SENSES OF TOUCH, TEMPERATURE, AND PAIN

The second largest cranial nerve, the trigeminal nerve, which is exceeded in size only by the auditory nerve, has a prominent ganglion. The sensory trigeminal complex is better represented than the general body somatosensory representation. The tactile thalamic region is reduced compared with that of many other mammals. The arcuate division is more developed than the external division, reflecting a greater representation of the face in animals that have relatively large heads.

Encapsulated nerve endings, especially numerous about the head and snout, around the blowhole, and encircling the anus and genital slit, are found in the superficial portion of the dermis (Palmer and Weddell, 1964; Harrison and Thurley, 1974). Fetal bottlenose dolphins have several hairs on either side of the snout or upper lip, but these fall out around the time of birth leaving only whisker pits barely visible in adult animals. On histological section, these pits can be seen to contain the remnants of the hair and a good nerve supply.

Several studies have been done on tactile sensivity of small odontocetes (Lende and Welker, 1972; Kolchin and Bel'kovich, 1973; Ridgway and Carder, 1989). Evoked potentials to stimuli such as vibrating, tapping, stroking, or dripping water on the skin have been recorded from the contralateral somatosensory cortex of the bottlenose dolphin (Lende and Welker, 1972). The areas of greatest skin sensitivity were on the head: the upper and lower lip near the commissure, around the eyes, and around the blowhole. Stimuli to the body trunk and tail produced very minimal evoked potentials. Soviet investigators used the galvanic skin response (GSR) to stimuli produced by a 0.3 mm weighted wire to make a partial map of body skin sensitivity in the common dolphin (Kolchin and Bel'kovich, 1973). Of the body portions studied, separate circular areas of about 5 cm diameter around the blowhole and eyes were most sensitive (10 mg/mm^2) while the snout, lower jaw, and melon were found to be somewhat less sensitive ($10–20 \text{ mg/mm}^2$); the skin along the back both anterior and posterior to the dorsal fin was even less sensitive ($20–40 \text{ mg/mm}^2$). The authors considered their values for the threshold of sensitivity to touch around the dolphin eyes and blowhole to be similar to those of a human in the most sensitive skin areas, namely, the tactile surfaces of the fingers, the skin of the eyelids, and the lips (Kolchin and Bel'kovich, 1973). Physiological mapping studies have located the somatosensory cortex of bottlenose dolphins in an area posterolateral to and bordering the motor cortex and anterior to and bordering the visual and auditory cortex (Supin et al., 1978).

No systematic studies have been done on pain perception or sensitivity to temperature; however, I have made rough observations during the veterinary care of bottlenose dolphins and have compared these with similar observations of domestic animals such as pigs or horses with which I have also had some experience. I have found that bottlenose dolphins are sensitive to pain to roughly the same extent as are pigs or horses and must be anesthetized for surgical procedures.

THE FACIAL NERVE

The main facial nucleus lateral to the superior olive is large and conspicuous (Breathnach, 1960). The dolphin facial nerve is well developed and apparently supplies the extensive musculature of the blowhole, nares, and nasal-sac system. Langworthy (1932) states, "The facial nucleus is large and the cells are subdivided into groups; each group apparently supplies a single muscle of the facial group." Since sound production is so important to animals that use echolocation and rely on sound for underwater communication, such development is not surprising.

THE SPINAL CORD

Because the spinal cord carries fibers to and from most of the body, most of the regulatory and body monitoring functions of the brain should be represented in the cord. Most reptiles and fish have more spinal cord than brain, while mammals have brains that are much heavier than the spinal cord. Worden (1951) proposed the ratio of brain weight

to spinal cord weight as an index of encephalization that might be correlated with intelligence across species. The brain to spinal cord ratio is higher in the bottlenose dolphin (Fig. 6) than in any other species measured thus far except for *Homo sapiens*. The ratio is about 50:1 in humans, 40:1 in bottlenose dolphins, 34:1 in Pacific white-sided dolphins, 26:1 in Dall porpoises, *Phocoenoides dalli*, 8:1 in the macaque monkey, *Macacus*, and about 4:1 in cats, *Felis domesticus* (Ridgway et al., 1966). [Wirz (1950) presented an index of cerebralization relating different parts of the brain that ranked odontocetes along with humans at the highest level]. Of course, whether or not the ratio of brain weight to spinal cord weight can be correlated with intelligence across species must be evaluated by independent behavioral and physiological means.

The spinal cord of one bottlenose dolphin ended at about the third lumbar vertebra (Ridgway, 1968). The spinal cord is nearly cylindrical throughout. The ventral columns of white matter are strongly developed. Clarke's columns are fused into a single median nucleus, at least in the caudal part. The pyramidal tract is very small. The cortical projection into the cord is rather small; however, there seems no doubt that corticospinal fibers are present and form a crossed projection. Muscle spindles have been identified in dorsal epaxial muscle; the morphology of the spindles

and neuromuscular junctions appeared similar to those of other mammals (Tulsi, 1975).

THE PINEAL, MAMMILLARY BODIES, AND PITUITARY

In numerous dissections of odontocete brains, I have never found the pineal body, which has been considered absent by most observers of the odontocete brain (Breathnach, 1960). There is one report of a small pineal (displacing about 1 cm^3) from a mysticete, the humpback whale, *Megaptera novaeangliae* (Gersch, 1938). The organ is also present in embryonic stages of the blue whale, *Balaenoptera musculus*. Gross examination of the bottlenose dolphin brain does not reveal mammillary bodies, but mammillary nuclei are recognized histologically. The pituitary is well developed. The adenohypophysis and neurohypophysis are completely separated by a dural septum.

THE CEREBELLUM

The absolute size of the cerebellum of the largest mysticetes, without free digits and presumably without fine movements, is huge, approximately
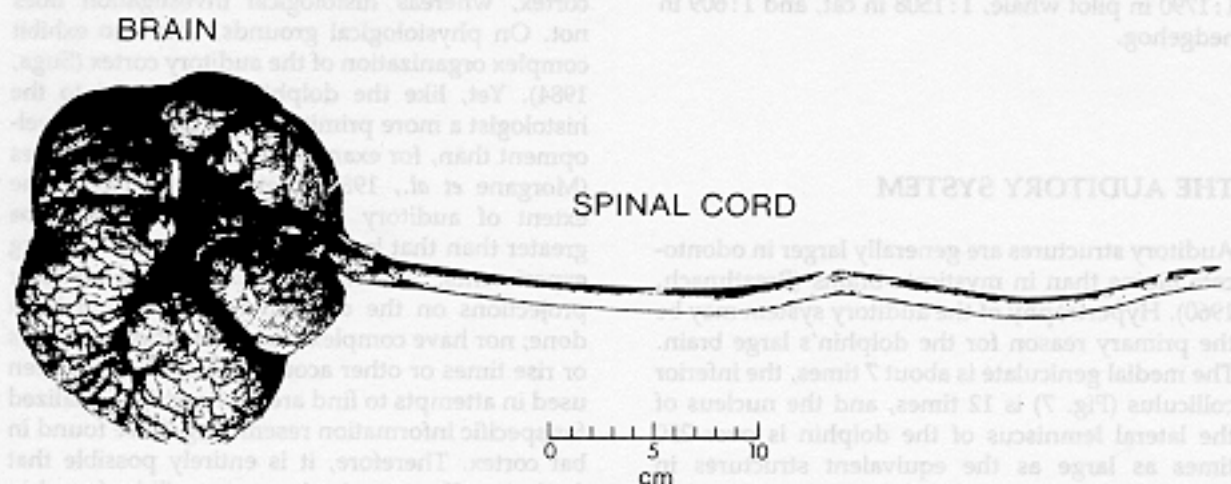
BRAIN

SPINAL CORD

Figure 6   Bottlenose dolphin brain and spinal cord which was dissected out as a unit. The cord ended at about the third lumbar vertebra. (From dissections by Robert F. Green and the author.)

1500 g. In these species, the cerebellum may be more than 20% of total brain weight; in the bottlenose dolphin, the cerebellum is more typically about 15% of total brain weight compared with about 11% in humans. In the embryonic stage, the dolphin cerebrum and cerebellum are about equal in width. According to paleontologists, the early forebears of modern cetaceans were the first giant mammals adapted to life-long swimming. Fossil studies have shown that these ancient cetaceans already had a very large cerebellum that was much wider than the cerebrum (Edinger, 1955). In modern odontocetes, the cerebrum has so enlarged as to cover the anterior portion of the cerebellum.

In comparison with the anatomy of the cerebellum of terrestrial mammals, the lobus simplex and paramedian lobule of the cetacean are much larger (Jansen and Jansen, 1969). The paraflocculus and nucleus interpositus, in these comparative terms, are enormous. The hemispheral parts of the anterior lobe, the flocculonodular lobe, the lateral nucleus, and the ansiform lobule are relatively small. In the same terms, the medial nucleus is moderately developed.

Lange (1975) has studied cell numbers and cell densities in the cerebellar cortex. He made comparisons between humans and various mammals, attaching particular significance to the ratio of Purkinje cells to granule cells. Lange found ratios of 1:2991 in human, 1:1898 in rhesus monkey, *Macaca mulatta*, 1:1812 in bottlenose dolphin, 1:1790 in pilot whale, 1:1508 in cat, and 1:609 in hedgehog.

THE AUDITORY SYSTEM

Auditory structures are generally larger in odontocete brains than in mysticete brains (Breathnach, 1960). Hypertrophy of the auditory system may be the primary reason for the dolphin's large brain. The medial geniculate is about 7 times, the inferior colliculus (Fig. 7) is 12 times, and the nucleus of the lateral lemniscus of the dolphin is over 250 times as large as the equivalent structures in humans (see Bullock and Gurevich, 1979). The ventral cochlear nucleus and some other brain stem nuclei also appear massive when compared with the human equivalents. The cetacean auditory nerve has several times as many fibers as the eighth nerve of man. Studies of fiber spectra have revealed larger myelinated fibers in odontocetes than in mysticete whales which in turn have larger eighth nerve fibers than humans. Fiber diameters have been measured using light microscopy. Plots of fiber diameters have shown that the largest numbers of fibers in the eighth nerve of the sperm whale, *Physeter catodon*, are aboout 9 μm in diameter, in the bottlenose dolphin about 7 μm, and in the fin whale about 5 μm (Jacobs and Jensen, 1964). Auditory tracts reaching the cerebral cortex are extensive. Some observers of the dolphin brain suggest that the cerebral cortex may have reached its great development on the basis of acoustic input (Langworthy, 1932; Wood and Evans, 1980).

Mapping the Auditory Cortex

Soviet investigators located extensive auditory projection areas on the dorsal surface of each hemisphere about 1.5–3.0 cm lateral to the sagittal fissure between the hemispheres (Supin *et al.*, 1978). Thus, compared with the brains of most land mammals, a difference appears in the dolphin's brain which indicates an apparent shifting of the auditory area from the temporal to the parietal lobe and the dorsum of the hemisphere. Data from evoked potential studies suggest the presence of both primary and secondary auditory cortex, whereas histological investigation does not. On physiological grounds, bats also exhibit complex organization of the auditory cortex (Suga, 1984). Yet, like the dolphin, bats reveal to the histologist a more primitive level of cortical development than, for example, carnivores or primates (Morgane *et al.*, 1986; Glezer *et al.*, 1988). The extent of auditory cortex in dolphins may be greater than that indicated in the Soviet mapping experiments. A tonotopic map of the cochlear projections on the dolphin cortex has not been done; nor have complex stimuli of different delays or rise times or other acoustic characteristics been used in attempts to find areas of cortex specialized for specific information resembling those found in bat cortex. Therefore, it is entirely possible that further auditory projection areas will be found in temporal cortex, which, in the dolphin, is less accessible than the dorsal area that has been mapped.
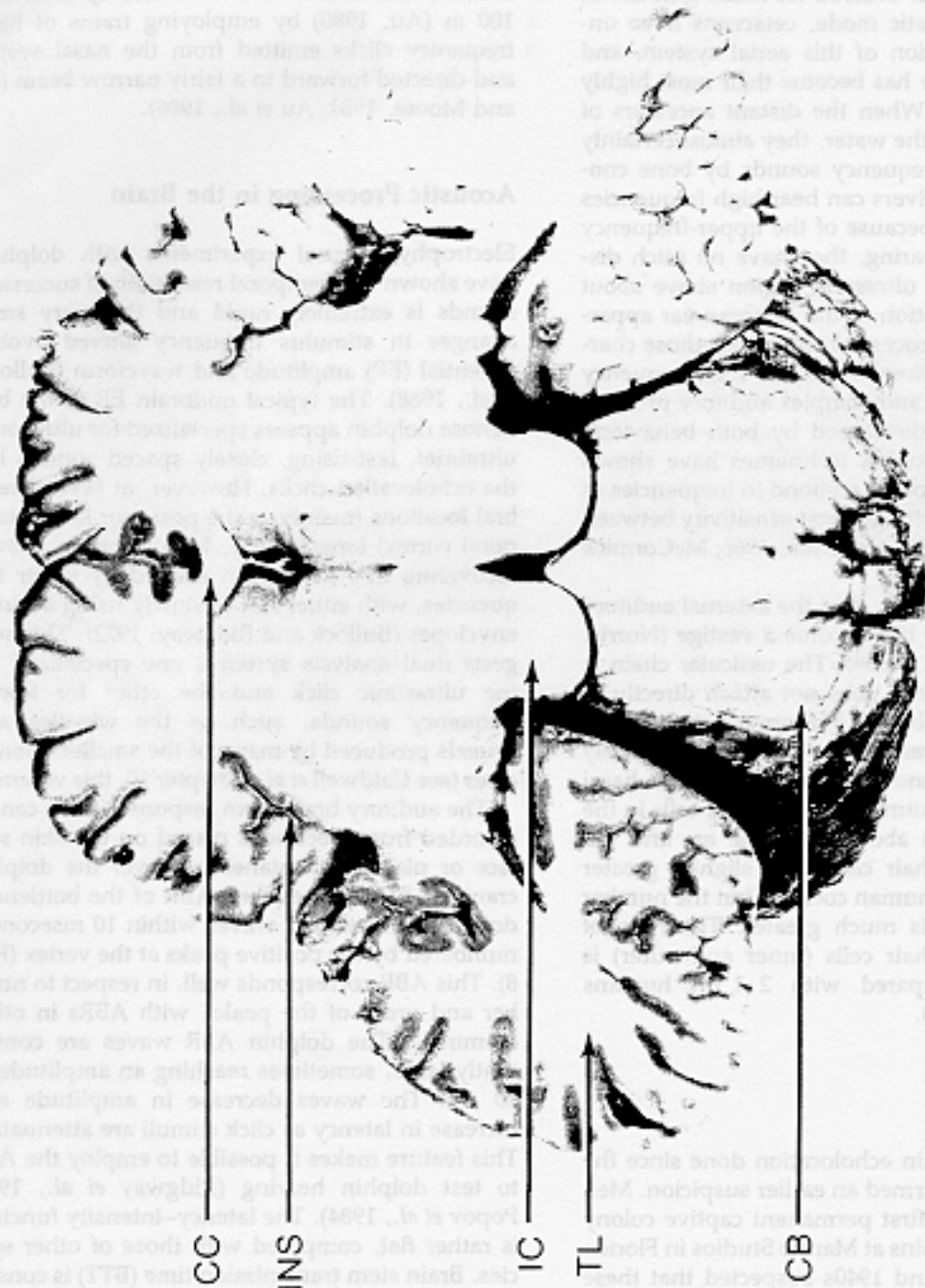
Hearing and the Ear

The mammalian ear evolved for hearing in air. In assuming the aquatic mode, cetaceans have undergone modification of this aerial system, and hearing apparently has become their most highly developed sense. When the distant ancestors of cetaceans entered the water, they almost certainly could hear high-frequency sounds by bone conduction. Human divers can hear such frequencies underwater, but, because of the upper-frequency limit of human hearing, the extent to which discrimination in the ultrasonic domain have about 20 kHz. The evolution of the cetacean ear apparatus became a process ...

Figure 7 Horizontal section through the brain (1901 g) of a Pacific bottlenose dolphin. CC, Corpus callosum; INS, insula; IC, inferior colliculus; TL, temporal lobe; CB, cerebellum. (Section by Robert F. Green.)

Hearing and the Ear

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The pinna is lacking, and the external auditory meatus apparently has become a vestige (Norris, 1968; Bullock et al., 1968). The ossicular chain is stiff, and the malleus does not attach directly to the tympanic membrane (McCormick et al., 1970). The basilar membrane of the cochlea is relatively long (35–40 mm) and very narrow near the basal end (25 μm). The number of inner hair cells in the dolphin cochlea is about the same as, and the number of outer hair cells only slightly greater than, those in the human cochlea, but the number of ganglion cells is much greater. The ratio of ganglion cells to hair cells (inner and outer) is roughly 5:1 compared with 2:1 in humans (Wever et al., 1971).

Echolocation

Research on dolphin echolocation done since the late 1950s has confirmed an earlier suspicion. Men who collected the first permanent captive colony of bottlenose dolphins at Marine Studios in Florida in the late 1930s and 1940s suspected that these animals possessed some sort of sonar or echolocation ability (McBride, 1956). Subsequent studies (Kellogg, 1958; Norris et al., 1961; Evans and Powell, 1967) have shown that blindfolded bottlenose dolphins can make extremely fine discriminations over underwater distances up to at least 100 m (Au, 1980) by employing trains of high-frequency clicks emitted from the nasal system and directed forward in a fairly narrow beam (Au and Moore, 1984; Au et al., 1986).

Acoustic Processing in the Brain

Electrophysiological experiments with dolphins have shown that temporal resolution of successive sounds is extremely rapid and that very small changes in stimulus frequency altered evoked potential (EP) amplitude and waveform (Bullock, et al., 1968). The typical midbrain EP of the bottlenose dolphin appears specialized for ultrasonic, ultrabrief, fast-rising, closely spaced sounds like the echolocation clicks. However, at several cerebral locations (mainly in the posterior lateral temporal cortex) long latency, long duration, slowly recovering EPs have been evoked by lower frequencies, with either fast or slowly rising acoustic envelopes (Bullock and Ridgway, 1972). This suggests dual analysis systems, one specialized for the ultrasonic click and the other for lower-frequency sounds, such as the whistles and squeals produced by many of the smaller odontocetes (see Caldwell et al., Chapter 10, this volume).

The auditory brain stem response (ABR) can be recorded from electrodes placed on the skin surface or placed subcutaneously over the dolphin cranium. The click-evoked ABR of the bottlenose dolphin consists of 7 waves within 10 mseconds, numbered by the positive peaks at the vertex (Fig. 8). This ABR corresponds well, in respect to number and order of the peaks, with ABRs in other mammals. The dolphin ABR waves are consistently large, sometimes reaching an amplitude of 10 μV. The waves decrease in amplitude and increase in latency as click stimuli are attenuated. This feature makes it possible to employ the ABR to test dolphin hearing (Ridgway et al., 1981; Popov et al., 1984). The latency–intensity function is rather flat, compared with those of other species. Brain stem transmission time (BTT) is considerably faster in the bottlenose dolphin (with a mean brain weight around 1500 g) than in humans or domestic cats and is similar to that of the rat
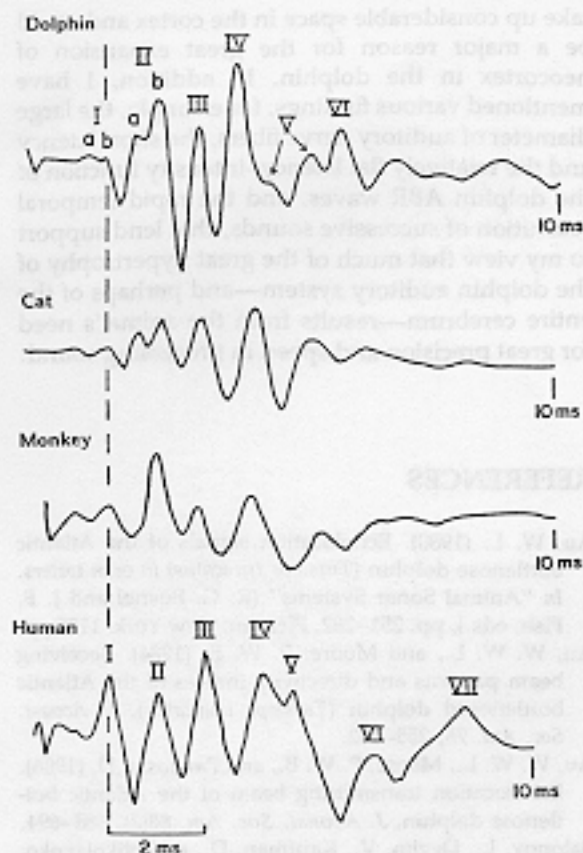
Figure 8 Comparison of a typical dolphin auditory brain stem response (ABR) with ABRs from cat, monkey, and human. All responses represent a 10-msecond time base which is slightly different for each species. The vertical broken line at the left passes through presumably similar components, the auditory nerve deflection, Wave I. (From Ridgway et al., 1981.)

(Ridgway et al., 1981). Despite a much longer nerve pathway, BTT in the dolphin is equal to or faster than that in much smaller-brained species. It has been suggested that, owing to larger auditory myelinated-fiber diameters, the axonal conduction velocity is higher by just enough to compensate for a longer path in the dolphin brain stem (Ridgway et al., 1981).

An interesting problem that might be investigated with the ABR concerns the increase in fiber diameter with increasing brain size. The largest delphinid, the killer whale, *Orcinus orca*, has a brain about four times larger than that of the bottlenose dolphin (6000 versus 1500 g) and perhaps ten times larger than those of some smaller delphinids. BTT in this large brain may be kept short by increased fiber diameters in the auditory pathway.

The above findings suggest that the dolphin brain is specialized for rapid processing of auditory stimuli (see also Bullock et al., 1968; Bullock and Ridgway, 1972). If given enough time, the human auditory system seems to perform as well on some echolocation tasks (Fish et al., 1976). Indeed, when pulses similar to dolphin echolocation pulses were projected at targets by instrumented divers and the received echoes stretched 128 times (tantamount to a slowed-down tape recording and therefore reduced equivalently in frequency), human divers performed with as few errors as bottlenose dolphins in distinguishing metal targets of copper, brass, or aluminum and geometrical aluminum shapes covered with neoprene rubber (Fish et al., 1976).

Studies with static metal targets may give only limited detail of the dolphin's echolocation processing ability. For example, the unnatural targets could well be a factor. However, if the findings of Fish et al. (1976) are a fair comparison of echolocation ability and based on a sonar discrimination task that is difficult for dolphins (and I have some doubt that they are), we must conclude that the major accomplishment in the sonar processing component of the dolphin auditory system is the ability to process sound rapidly.

Mackay (1967) has suggested that dolphins may employ phase information in sonar detection. Johnson (1967) has elaborated on the advantages of phase detection for echolocation by dolphins (Evans and Powell, 1967; Au, 1980). Wever et al. (1971) suggested that "the representation of detailed high frequency sounds, and especially their time and phase relations, may well be the basis for the dolphin's remarkable facility in echolocation." Since no proof existed, however, that the dolphin auditory system is sensitive to phase at the high frequencies used in echolocation target detection, we attempted to test the dolphin capability for phase detection using the ABR (Ridgway et al., 1981). Reversing the phase of single sine waves delivered to the hydrophone revealed a small but consistent difference in response between initial compression clicks versus initial rarefaction clicks,

suggesting that the dolphin auditory system might be capable of detecting phase even at high frequencies.

Suga's (1984) research has revealed an intricate organization of auditory cortex in bats, and he has suggested not only that equally complex organization may be present in other auditory systems of animals but also that human auditory cortex may show similar arrangements for processing the complex sounds of speech. In Suga's bats, complex sounds are processed by neurons tuned to combinations of information-bearing elements or parameters in the sounds. For example, areas of cortex are tuned to particular echo delays and particular echo amplitudes. Neurons tuned to specific information-bearing parameters (IBPs) or combinations of IBPs are clustered in areas of the cerebral cortex and systematically arranged along axes or in coordinate systems for representation of sounds that are biologically important to the species (Suga, 1984).

It seems likely that equally complex sound processing takes place in the dolphin cortex. If so, the mapping experiments conducted to date (Supin et al., 1978), though they showed certain differences of response in three areas of auditory cortex, may not have been of sufficient acoustic detail to reveal systematically arranged axes of specific delay-sensitive or amplitude-sensitive neurons and thus do not reveal the full extent of cortical organization. Possibly, surface segments that were not responsive in the mapping experiments (Supin et al., 1978) contain neurons tuned to more specific acoustic parameters than those tested.

Detailed organization of auditory cortex described for bats may be equally or even more complex in dolphins. If so, the dolphin cortex must map an extensive surrounding area of the environment with specific acoustic parameters. According to Suga (1984), mustached bats (Pteronotus parnellii) map an area of only about 3 m, and target distances of 50–140 cm are best represented; on the other hand, dolphins, with an echolocation range of 100 m or more, probably map a large area of their surroundings for specific acoustic parameters. Since sound travels over four times as fast in water, neurons performing equal echo delays of X mseconds will represent Y m in a bat and $4Y$ m in a dolphin. Specific neurons forming such axes may

take up considerable space in the cortex and could be a major reason for the great expansion of neocortex in the dolphin. In addition, I have mentioned various findings, for example, the large diameter of auditory nerve fibers, the short latency and the relatively flat latency–intensity function of the dolphin ABR waves, and the rapid temporal resolution of successive sounds, that lend support to my view that much of the great hypertrophy of the dolphin auditory system—and perhaps of the entire cerebrum—results from the animal's need for great precision and speed in processing sound.

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